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Published in:

Methods in Ecology and Evolution

DOI:

[10.1111/2041-210x.12804](https://doi.org/10.1111/2041-210x.12804)

Publication date:

2017

Document Version

Publisher's PDF, also known as Version of record

[Link to publication](#)

Citation for pulished version (HARVARD):

Baert, JM, Jaspers, S, Janssen, CR, De Laender, F & Aerts, M 2017, 'Nonlinear partitioning of biodiversity effects on ecosystem functioning', *Methods in Ecology and Evolution*, vol. 8, no. 10, pp. 1233-1240.
<https://doi.org/10.1111/2041-210x.12804>

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Nonlinear partitioning of biodiversity effects on ecosystem functioning

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Summary

1. Assessing the consequences of biodiversity changes for ecosystem functioning requires separating the net effect of biodiversity from potential confounding effects such as the identity of the gained or lost species. Additive partitioning methods allow factoring out these species identity effects by comparing species' functional contributions against the predictions of a null model under which functional contributions are independent of biodiversity.
2. Classic additive partitioning methods quantify biodiversity effects based on a linear relationship between species deviations from the null model and their functional traits. However, based on ecological theory, nonlinear relationships are also possible.
3. Here, we demonstrate how additive-partitioning methods can be extended to describe such nonlinear relationships, and explain how nonlinear biodiversity effects can be interpreted.
4. We apply both linear and nonlinear partitioning methods to the Cedar Creek Biodiversity II experiment. Nonlinear relationships were detected in the majority of plots, and increased with diversity. Nonlinear partitioning thereby identified a convex relationship between species functional traits and their deviations from the null model, driven by strong positive effects of both species with low and high functional trait values on ecosystem functioning.
5. The presented nonlinear extension of additive partitioning methods is therefore essential for revealing more complex biodiversity effects on ecosystem functioning, that are likely to occur in biodiversity experiments.

Key-words: biodiversity, community ecology, ecosystem functioning, statistics

Introduction

Anthropogenic activities are causing unprecedented global biodiversity changes with potential major consequences for ecosystem function provisioning (Hooper *et al.* 2012; Pimm *et al.* 2014; De Laender *et al.* 2016). Understanding how biodiversity and ecosystem functioning are interrelated has therefore become a major objective in ecology. Since the 1990s, hundreds of studies have assessed the biodiversity–ecosystem–functioning relationship by randomly assembling communities of different levels of species richness from a common species pool (Schulze & Mooney 1993; Chapin *et al.* 1997; Loreau *et al.* 2001; Hooper *et al.* 2005; Cardinale *et al.* 2012). However, the increased likelihood of sampling species with favourable traits in the high diversity treatments can thereby bias regression analysis (Aarssen 1997; Huston 1997, 2000; Wardle 1999). Because both the number and identity of species can influence ecosystem functioning, estimating the biodiversity–ecosystem functioning relationship requires high replication to control for the effect of species identities (Tilman 1997).

Additive partitioning methods allow directly factoring out the effect of species identities, using a null model (Loreau & Hector 2001; Fox 2005). Under the null hypothesis that the strengths of inter- and intraspecific interactions are equal, species functioning is independent of the identity and number of species in the system. Observed deviations from this null model can then be partitioned between two (Loreau & Hector 2001) or three (Fox 2005) terms that reflect various classes of mechanisms through which biodiversity can affect ecosystem functioning. Contrary to classic regression analyses that estimate biodiversity effects by comparing ecosystem functioning across a species richness gradient, additive partitioning methods thus estimate biodiversity effects based on a system-specific prediction of ecosystem functioning in the absence of biodiversity effects.

Current additive partitioning methods assume a linear relationship between species deviations from the null model and their functional traits (Loreau & Hector 2001; Fox 2005). However, based on ecological theory, there is *a priori* no reason to assume the relationship between species deviations from the null model and functional traits should be linear. For example, nonlinear relationships have shown to arise over time when ecosystem functioning becomes increasingly driven by particular (groups of) species (e.g. Li *et al.* 2010). Although a linear

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relationship quantifies the general pattern, including higher order terms allows more accurately describing deviations from the null model, and consequently leads to a more comprehensive treatment of biodiversity effects on ecosystem functioning.

Here, we first demonstrate how current additive partitioning methods can be extended with higher order terms to include nonlinear dependencies between species' deviations from the null model and their functional traits. Next, we explain how these higher order terms can be interpreted. Finally, we apply nonlinear additive partitioning methods to data from the Cedar Creek Biodiversity II experiment to illustrate the occurrence of nonlinear biodiversity effects, and discuss how the nonlinear partitioning results in a more detailed insight into the effect of biodiversity on ecosystem functioning.

Linear additive partitioning methods

Many ecosystem functions are the aggregate of the individual species' functional contributions (e.g. primary production, nutrient retention or total biomass). Under the null hypothesis that inter- and intraspecific interactions are equal, the functional contribution of an individual is independent of the identity of the individuals with which it interacts. As the system behaves neutrally under the null hypothesis, species functional contributions undergo a random walk. Species are hence expected to function equally well in monocultures as in mixed cultures. The expected value of a species' functional contribution to ecosystem functioning therefore equals its initial fraction in the mixed culture times its contribution in monoculture (Loreau & Hector 2001; Fox 2005). For a system containing n species, the expected value of an aggregated ecosystem function or yield (Y_e) under the null hypothesis can thus be expressed as (Loreau & Hector 2001):

$$Y_e = \sum_{i=1}^n Y_{e,i} = \sum_{i=1}^n \frac{Y_{o,i}}{M_i} M_i = \sum_{i=1}^n RY_{e,i} M_i. \quad \text{eqn 1}$$

$Y_{e,i}$ is the expected individual species yield, which can also be expressed as the realised fraction of the species monoculture yield (M_i), the relative yield ($RY_{e,i}$). As the system behaves neutrally, the expected relative yield remains constant over time. Note that the term 'yield' is used to refer to any measurable ecosystem function or a species functional contribution thereto, to comply with common terminology (Loreau & Hector 2001; Fox 2005). For any aggregated ecosystem function, the observed deviation in ecosystem functioning from the null model (ΔY) equals the sum of the deviations of the individual species observed yield (Y_o) or relative yield (RY_o) from the null model (Loreau & Hector 2001):

$$\begin{aligned} \Delta Y &= Y_o - Y_e = \sum_{i=1}^n Y_{o,i} - Y_{e,i} = \sum_{i=1}^n (RY_{o,i} - RY_{e,i}) M_i \\ &= \sum_{i=1}^n \Delta RY_i M_i. \end{aligned} \quad \text{eqn 2}$$

Loreau & Hector (2001) demonstrated that rewriting eqn (2) based on the expected value of the product of two

dependent variables, results in two terms that can be interpreted as reflecting the complementarity effect and selection effect:

$$\Delta Y = n E(\Delta RY) E(M) + n \text{cov}(\Delta RY, M). \quad \text{eqn 3}$$

The sign of the first term depends on the average species' deviation from the null hypothesis. The term becomes positive when species perform better on average in mixed cultures compared to monocultures, which is interpreted as the consequence of niche complementarity and/or facilitative interactions between species. The second term quantifies the linear dependency between species' deviations from the null model and their monoculture yields. Hence, this term is positive when species with the above average monoculture yields have on average a higher functional contribution to ecosystem functions, reflecting the effect of dominance of species with particular functional traits on ecosystem functioning. Note that throughout this paper, the term 'functional traits' will be used to refer to the species monoculture yields. Loreau & Hector (2001) therefore referred to the second term as the selection effect, mimicking the effect of natural selection in evolution as given by the Price equation (Price 1970). Fox (2005) demonstrated that the selection effect is only partially analogous to natural selection *sensu* Price (1970). The latter reflects changes in frequencies, whereas ΔRY_i is not limited to the [0;1] interval, nor needs $\sum \Delta RY_i$ to equal 1. Therefore, Fox (2005) proposed an alternative partitioning of species' deviations from the null-model:

$$\begin{aligned} \Delta Y &= \sum_{i=1}^n (RY_{o,i} - RY_{e,i}) M_i = \sum_{i=1}^n \left(\frac{RY_{o,i}}{RYT} - RY_{e,i} \right) M_i \\ &\quad + \sum_{i=1}^n \left(RY_{o,i} - \frac{RY_{o,i}}{RYT} \right) M_i. \end{aligned} \quad \text{eqn 4}$$

Under the assumption that the number of individuals in the system is independent of species richness, that is, a substitutive design, the expected relative yield ($RY_{e,i}$) equals the species' initial proportion in the mixture. By dividing the observed relative yield by the relative yield total ($RYT = \sum RY_{o,i}$), the first term of eqn (4) thus now does represent the changes from species' initial frequencies. Analogous to eqn (2), eqn (4) can be rewritten as (Fox 2005):

$$\begin{aligned} \Delta Y &= n E(\Delta RY) E(M) + n \text{cov} \left(\frac{RY_{o,i}}{RYT} - RY_{e,i}, M \right) \\ &\quad + n \text{cov} \left(RY_{o,i} - \frac{RY_{o,i}}{RYT}, M \right). \end{aligned} \quad \text{eqn 5}$$

This additive partitioning presented by Fox (2005) now splits the selection effect into two covariance terms: the dominance effect and the trait-dependent complementarity effect. The first covariance term quantifies the extent by which deviations from the expected frequency linearly depend on their monoculture yield. Changes in species frequencies imply that the increase in one species necessarily results in the decrease of other species. Consequently, the first term reflects changes in ecosystem functioning by dominance of species with particular functional traits, analogous to natural selection *sensu* Price

(1970). The second covariance term, the trait-dependent complementarity effect, quantifies the linear dependency between species' monoculture yields and the extent to which species relative yields do not result from replacement. Hence, this term is interpreted as reflecting the effect of asymmetrical species complementarity that occurs depending on species functional traits. This in contrast to the first term of eqn (5) is identical to the complementarity effect by Loreau & Hector (2001), and depends on the average deviation from the null model, which occurs irrespective of species monoculture yields. This term is hence also referred to as the trait-independent complementarity effect (Fox 2005).

Nonlinearly extending additive partitioning methods

Both the bi- (Loreau & Hector 2001) and tripartite (Fox 2005) method are based on the expected value of the product of two dependent variables. These methods use covariances (eqns 3 and 5), measuring the linear dependence between deviations from the null model and species functional traits (i.e. monoculture yields). To extend additive partitioning methods with higher order terms, we introduce a generic function $g(\tilde{M}_i, \Theta)$ describing the relationship between the deviation of species functional contribution from that expected under the null hypothesis that inter- and intraspecific interactions are equal, and their centred monoculture yields, $\tilde{M}_i = M_i - E(M)$:

$$\Delta RY_i - E(\Delta RY) = g(\tilde{M}_i, \Theta) + \varepsilon_i \quad \text{eqn 6}$$

Θ is a vector containing the unknown parameters of the function g and ε_i is the model error term for species i . Fitting this model to data with ordinary least squares leads to the identity

$$\Delta RY_i - E(\Delta RY) = g(\tilde{M}_i, \hat{\Theta}) + e_i, \quad \text{eqn 7}$$

to the least squares estimate $\hat{\Theta}$ for Θ , and to the residuals

$$e_i = [\Delta RY_i - E(\Delta RY)] - g(\tilde{M}_i, \hat{\Theta}) \quad i = 1, \dots, n. \quad \text{eqn 8}$$

Note that the function g has a zero intercept as the mean deviation from the null hypothesis is subtracted from species deviation from the null hypothesis in eqn (6). The function g is thus centred on the mean deviation from the null hypothesis and the mean monoculture yield, so that all terms depend on \tilde{M}_i . Inserting identity 7, eqn (2) can now be written as:

$$\begin{aligned} \Delta Y &= \sum_{i=1}^n [\Delta RY_i - E(\Delta RY)] M_i + \sum_{i=1}^n E(\Delta RY) M_i \\ &= \sum_{i=1}^n g(\tilde{M}_i, \hat{\Theta}) \tilde{M}_i + \sum_{i=1}^n e_i \tilde{M}_i + n E(\Delta RY) E(M) \end{aligned} \quad \text{eqn 9}$$

If the relationship between species deviations from the null model and the monoculture yield is linear, i.e. $g(\tilde{M}_i, \hat{\Theta}) = \hat{\theta}_1 \tilde{M}_i$, it follows from ordinary least squares theory that $\sum_{i=1}^n e_i \tilde{M}_i = 0$, and consequently equation 9 then becomes:

$$\begin{aligned} \Delta Y &= \hat{\theta}_1 \sum_{i=1}^n \tilde{M}_i^2 + n E(\Delta RY) E(M) \\ &= n \hat{\theta}_1 s_M^2 + n E(\Delta RY) E(M) \\ &= n \text{cov}(\Delta RY, M) + n E(\Delta RY) E(M) \end{aligned} \quad \text{eqn 10}$$

This is the additive partitioning by Loreau & Hector (2001). Note that $\hat{\theta}_1$, the optimal least square estimate of θ_1 , equals $\frac{\text{cov}(\Delta RY, M)}{s_M^2}$ and that s_M^2 is the sample variance of the species monoculture yields. Analogously, eqn (4) can be written as:

$$\begin{aligned} \Delta Y &= \sum_{i=1}^n g^{(1)}(\tilde{M}_i, \hat{\Theta}^{(1)}) \tilde{M}_i + \sum_{i=1}^n \varepsilon_i^{(1)} \tilde{M}_i \\ &\quad + \sum_{i=1}^n g^{(2)}(\tilde{M}_i, \hat{\Theta}^{(2)}) \tilde{M}_i + \sum_{i=1}^n \varepsilon_i^{(2)} \tilde{M}_i \\ &\quad + n E(\Delta RY) E(M) \end{aligned} \quad \text{eqn 11}$$

whereby, similar to identity (7):

$$\frac{RY_{o,i}}{RYT} - RY_{e,i} - E\left(\frac{RY_o}{RYT} - RY_e\right) = g^{(1)}(\tilde{M}_i, \hat{\Theta}^{(1)}) + e_i^{(1)} \quad \text{eqn 12}$$

and

$$RY_{o,i} - \frac{RY_{o,i}}{RYT} - E\left(RY_o - \frac{RY_o}{RYT}\right) = g^{(2)}(\tilde{M}_i, \hat{\Theta}^{(2)}) + e_i^{(2)}. \quad \text{eqn 13}$$

Note that $g^{(1)}$ describes deviations from the expected frequency (i.e. the dominance effect) and that $g^{(2)}$ describes deviations that are not associated with changes in frequency (i.e. the trait-dependent complementarity effect). Hence, when $g^{(1)}(\tilde{M}_i, \hat{\Theta}^{(1)}) = \hat{\theta}_1^{(1)} \tilde{M}_i$ and $g^{(2)}(\tilde{M}_i, \hat{\Theta}^{(2)}) = \hat{\theta}_1^{(2)} \tilde{M}_i$, eqn (11) equals eqn (5), which is the partitioning presented by Fox (2005). When $g(\tilde{M}_i, \hat{\Theta})$, $g^{(1)}(\tilde{M}_i, \hat{\Theta}^{(1)})$ and $g^{(2)}(\tilde{M}_i, \hat{\Theta}^{(2)})$ are m^{th} order polynomials, eqns (9) and (11) can be written as:

$$\begin{aligned} \Delta Y &= \hat{\theta}_1 \sum_{i=1}^n \tilde{M}_i^2 + \hat{\theta}_2 \sum_{i=1}^n \tilde{M}_i^3 + \dots \\ &\quad + \hat{\theta}_m \sum_{i=1}^n \tilde{M}_i^{m+1} + n E(\Delta RY) E(M), \end{aligned} \quad \text{eqn 14}$$

and

$$\begin{aligned} \Delta Y &= \left\{ \hat{\theta}_1^{(1)} \sum_{i=1}^n \tilde{M}_i^2 + \hat{\theta}_2^{(1)} \sum_{i=1}^n \tilde{M}_i^3 + \dots + \hat{\theta}_{m^{(1)}}^{(1)} \sum_{i=1}^n \tilde{M}_i^{m^{(1)}+1} \right\} \\ &\quad + \left\{ \hat{\theta}_1^{(2)} \sum_{i=1}^n \tilde{M}_i^2 + \hat{\theta}_2^{(2)} \sum_{i=1}^n \tilde{M}_i^3 + \dots + \hat{\theta}_{m^{(2)}}^{(2)} \sum_{i=1}^n \tilde{M}_i^{m^{(2)}+1} \right\} \\ &\quad + n E(\Delta RY) E(M). \end{aligned} \quad \text{eqn 15}$$

These equations now partition the selection effect (eqn 14) or the dominance effect and trait-dependent complementarity effect (eqn 15) in m terms, describing the first up to the m^{th} order dependency of the deviation from the null hypothesis on

species' monoculture yields. As eqns (3, 5, 14 and 15) are decompositions of ΔY , the sum of the m terms in eqns (14) and (15) still equals the covariance terms in the partitioning methods of Loreau & Hector (2001) and Fox (2005).

The use of m^{th} order polynomials to describe the relationship between species monoculture yields and deviations from the null model allow for a more versatile analysis of species deviations from the null model. When sufficient data is available, it allows distinguishing between the linear, quadratic and up to m^{th} order deviations from the null model. However, as most biodiversity experiments only include a limited number of species (rarely over 16 species), fitting third or higher order polynomials can result in over fitting. In addition, first and second-order terms can more easily be ecologically interpreted than higher order terms. First-order terms describe how species with above average monoculture yields differ in their deviation from the null model compared to species with below average monoculture yields. When the first-order regression coefficient ($\hat{\theta}_1$) is positive, species with higher monoculture yields deviate more from the null model than the average deviation, taken across all species in the system (Fig. 1, right panel). Analogously, species with lower monoculture yields deviate more than average from the null model when the first-order regression coefficient is negative (Fig. 1, left panel). The second-order regression coefficient describes to what extent the deviation from the null model is non-linearly related to monoculture yield. They therefore represent a parabolic relationship and the sign of the second-order regression coefficient ($\hat{\theta}_2$) determines whether the parabola is convex ($\hat{\theta}_2 > 0$) or concave ($\hat{\theta}_2 < 0$). The straight line described by the first-order regression coefficient is the tangent of this parabola at the point $(\bar{M}, \overline{\Delta RY})$. Both first and second-order regression coefficients determine the position of the tip of the parabola ($-\hat{\theta}_1/2\hat{\theta}_2$). When the tip of the parabola lies inside the monoculture range, the relationship is unimodal (Fig. 1 concave relationship in the left panel, or convex relationship in the right panel). As the tip of the parabola shifts away from the monoculture range, the

deviations from the linear relationship become more asymmetrical (Fig. 1). In these extreme cases, the second-order term describes to what extent species with high or low monoculture yield deviate from the linear term. When the tip of the parabola lies closer to the average monoculture range, relationships become more symmetrical and so describe to what extent both species with low and high monoculture yields deviate from the linear relationship. When this tip lies outside the monoculture range (Fig. 1, convex relationship in the left panel, or concave relationship in the right panel), the second-order polynomial describes a monotonic relationship.

Application and occurrence of nonlinear biodiversity effects

The Cedar Creek Biodiversity II experiment is a field experiment conducted to assess the effects of species diversity on grassland productivity by randomly assembling systems of 1, 2, 4, 8, and 16 species from a pool of 18 grassland perennials (Tilman *et al.* 2001; Tilman, Reich & Knops 2006). We analysed 13 years of data gathered between 2001 and 2013. To avoid strong effects of species loss or gain on ecosystem functioning, we only included plots for which a minimum of 75% of the original species were still present and for which colonisation by new species had limited effects on the total above-ground biomass. We applied a partitioning based on linear relationships (Loreau & Hector 2001; Fox 2005) and an extension of these methods based on second-order polynomials to the data and tested which relationship described the observed deviations from the null model best (F -ratio test using a 5% significance level, assuming normality of model residuals, Fig. S1, Supporting Information). To be able to fit second-order polynomials, only plots with an initial species richness of at least four species were considered. Higher order polynomials were not considered due to constraints in the maximal degrees of freedom.

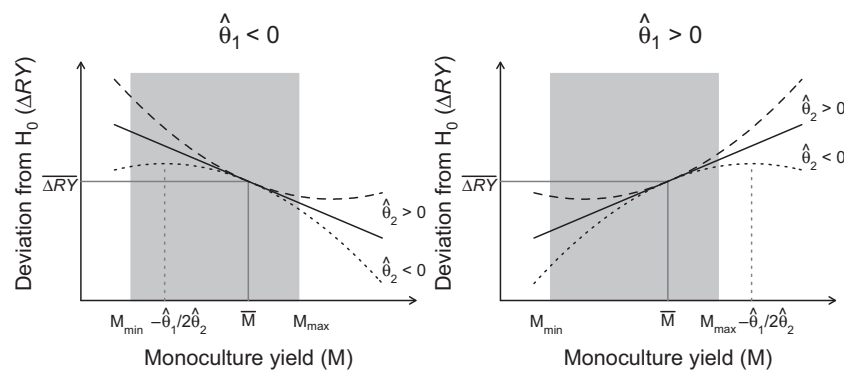


Fig. 1. Linear and quadratic deviations from the null model. The first-order regression coefficient determines whether the general relationship between species deviations from the null model and the monoculture yield is negative (left) or positive (right). The second-order regression coefficient determines whether the relationship is convex $\hat{\theta}_2 > 0$ or concave $\hat{\theta}_2 < 0$. Whether the relationship is unimodal or monotonic depends on whether the tip of the parabola ($-\hat{\theta}_1/2\hat{\theta}_2$) is located within the species monoculture range (indicated in grey) or not, respectively. M_{\min} and M_{\max} are, respectively, the minimum and maximum monoculture yield. Note that the linear relationship between species monoculture yields and deviations from the null model of linear additive partitioning methods is tangent to the parabola at the average deviation from the null model ($\overline{\Delta RY}$) and average monoculture yield (\bar{M}).

Second-order polynomials fitted deviations from the null model better in most plots. Partitioning deviations between the selection and complementarity effect (Loreau & Hector 2001) revealed that in 69 of the 91 plots selection effects were better described by second-order polynomials in at least one of the years. The number of plots in which second-order polynomials fitted selection effects significantly better increased with diversity (Kruskal–Wallis $\chi^2_2 = 177.3$, $P < 0.001$). In 17 out of the 35 plots containing 16 species, second-order polynomials fitted selection effects better in at least half of the years (Fig. 2). For systems of 4 and 8 species, second-order polynomials fitted selection effects better for at least half of the years in only 3 out of the 30 and 2 out of the 26 plots, respectively. The nonlinearity in selection effects was caused by the non-linearity of the trait-dependent complementarity effects sensu Fox (2005) (Fig. 2). The results found for trait-dependent complementarity effects were similar to those found for the selection effect: the number of plots in which deviations were better described by second-order polynomials increased with diversity (Kruskal–Wallis $\chi^2_2 = 191.1$, $P < 0.001$).

In highly diverse systems, linear additive partitioning methods underestimate the deviations from the null model for species driving productivity (Fig. 3). Diversity increases the number, and thus potentially the complexity, of species interactions. Competition for nitrogen plays an important role in grasslands (e.g. Tilman, Wedin & Knops 1996; Tilman *et al.* 1997; Hille Ris Lambers *et al.* 2004). The presence of nitrogen fixing legumes has therefore a significant impact on the system's productivity by increasing the amount of nitrogen available, and thus the potential for species to over yield (i.e. a positive ΔRY). Hence, strong competitors for nitrogen are expected to benefit most from the presence of legumes (Hille Ris Lambers *et al.* 2004). Indeed, strong positive deviations from the null model occurred for the dominant grass species such as *Poa pratensis*, *Andropogon gerardi* and *Schizachyrium scoparium*, but also legumes overyielded in mixtures due to their nitrogen fixing abilities, reducing competition for nitrogen (Fig. 3, Tilman & Downing 1994; Hille Ris Lambers *et al.*

2004). Nonlinear partitioning methods thus captured deviations from the null model better for grasses with low monoculture yields, and legumes with high monoculture yields (Fig. 3). In systems where second-order polynomials described deviations from the null model best, first-order regression coefficients were almost invariably negative, whereas second-order regression coefficients were positive for both selection and trait-dependent complementarity effects (Fig. 4, upper panels). Although the symmetry of the relationship 1 differed among systems, all relationships are rather asymmetrical, with the tip of the parabola near the upper limit of the monoculture range, so that deviations from the null model were strongest for grass species with low monoculture yields (Figs 3 and 4).

Discussion

The nonlinear extension presented here increases the flexibility of additive partitioning methods. We demonstrate that nonlinear relationships between the deviation from the null model and functional traits are likely to occur in biodiversity experiments (Fig. 2). A more accurate description of this relationship by nonlinear additive partitioning methods therefore offers a more detailed insight into how biodiversity affects ecosystem functioning (Figs 3 and 4). In addition, the extension we propose can resolve leverage problems that can occur when fitting a linear model to nonlinear deviations from the null model.

Biodiversity experiments are often designed with equal initial functional contributions among species. This even initial condition does however not necessarily correspond to equilibrium conditions. Indeed, species interactions can change species functional contributions and biodiversity effects over time (e.g. Fargione *et al.* 2007). Here, we reveal that such strong nonlinear deviations from the initial conditions already occurred after a limited number of generations in the Biodiversity II grassland experiment (Fig. 2), and could thus be widespread in biodiversity studies.

How deviations from the null model relate to species monoculture yields depends on the type of interactions. For

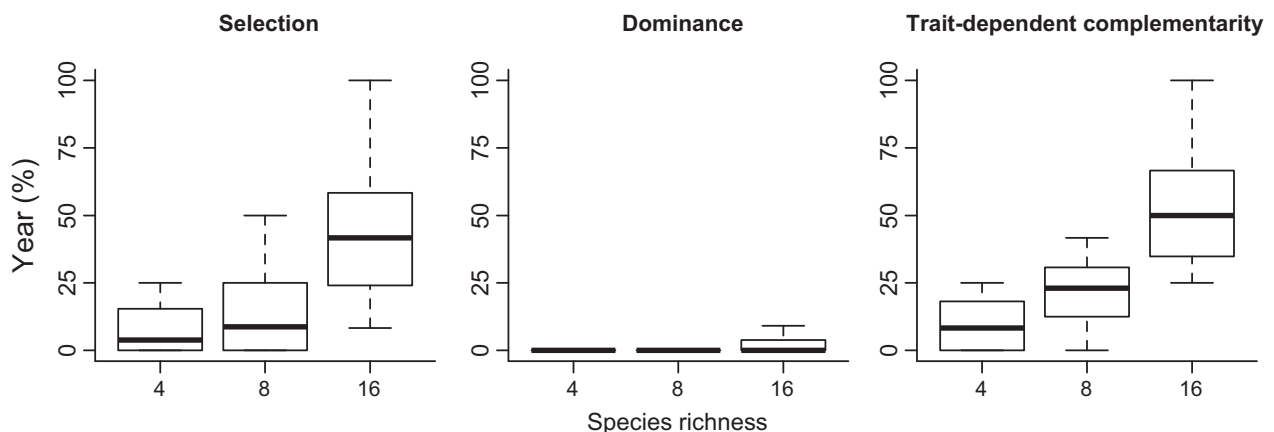


Fig. 2. Comparison between additive partitioning methods based on linear relationships and second-order polynomials. The percentage of years for which second-order polynomials fitted selection effects (Loreau & Hector 2001) and dominance and trait-dependent complementarity effects (Fox 2005) better than linear relationships (F -ratio test, $P < 0.05$).

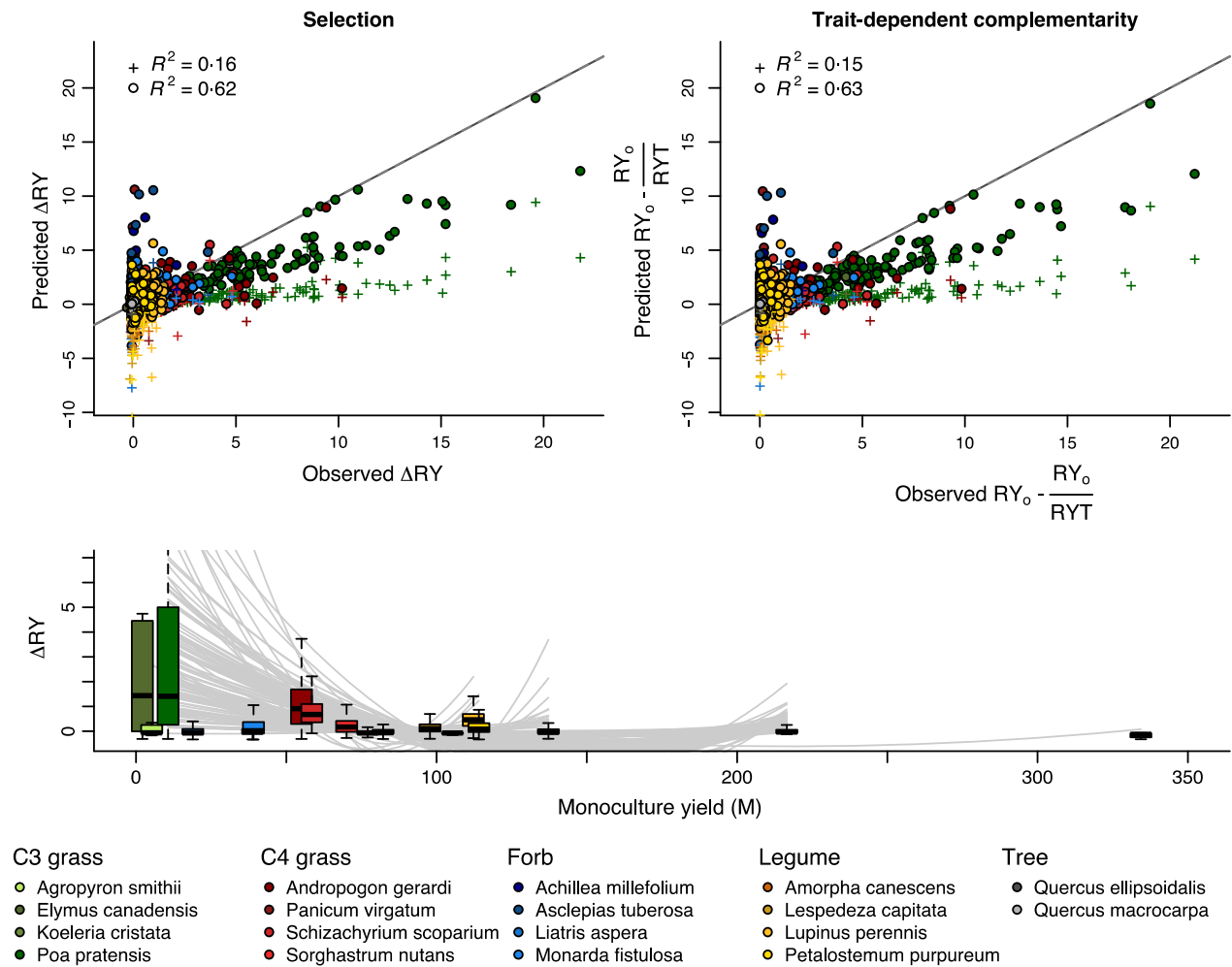


Fig. 3. Comparison of model performance between partitioning methods based on linear and second-order relationships. Upper panels represent the predicted deviations from the null model according to linear partitioning (+) and second-order partitioning methods (o), plotted against the observed deviations for the selection (left) and trait-dependent complementarity (right) effect. The lower panel represent the relationships between species deviation from the null model and the monoculture yield. Boxplot represent observed species deviations, and whiskers correspond to maximal 1.5 times the interquartile range. Grey lines represent the fitted second-order polynomials that fitted deviations from the null model significantly better than linear relationships (F -ratio test, $P < 0.05$).

example, legumes generally over yield in mixtures due to their nitrogen fixing ability, irrespective of community composition, whereas grasses over yield due to the positive effect of legumes (Hille Ris Lambers *et al.* 2004). The convex relationships between deviations from the null model and monoculture yield therefore primarily occurred in highly diverse treatments where legumes and grasses were both present. The nonlinear partitioning method presented here allows directly splitting the contribution of species with intermediate functional trait values from that of species with extreme functional trait values. Splitting selection or dominance and trait-dependent complementarity effects in first and second-order terms does not change the total strength of these effects as calculated by linear additive partitioning methods. However, it does allow a more detailed understanding of how biodiversity affects ecosystem functioning in a single analysis. Depending on the symmetry of the parabola, the second-order term quantifies the effect of species with low, high or both functional trait values (Fig. 1). Moreover, as these linear and higher-order partitioning

methods represent a nested set of models, it can easily be formally tested if higher-order extensions, and thus the additional inclusion of parameters in the model, are warranted.

One limitation of our extension is that the use of second-order polynomials is limited to systems with at least three species, whereas linear additive partitioning methods can also be applied to systems with two species. Many biodiversity experiments use systems with two species as the lowest diversity level, and so the approach we present will not be applicable to these low-diversity cases. In more diverse systems, however, nonlinear partitioning methods can help to avoid several statistical issues that can occur when fitting an inappropriate model structure to the data. When species deviations from the null model are nonlinear, the estimated regression coefficients of a linear regression can be strongly affected by outliers (Seber & Lee 2003). Outliers can therefore have severe effects on the magnitude, and particularly the sign (which alters their ecological interpretation) of selection, dominance or trait-dependent complementarity effects. Species with extremely low

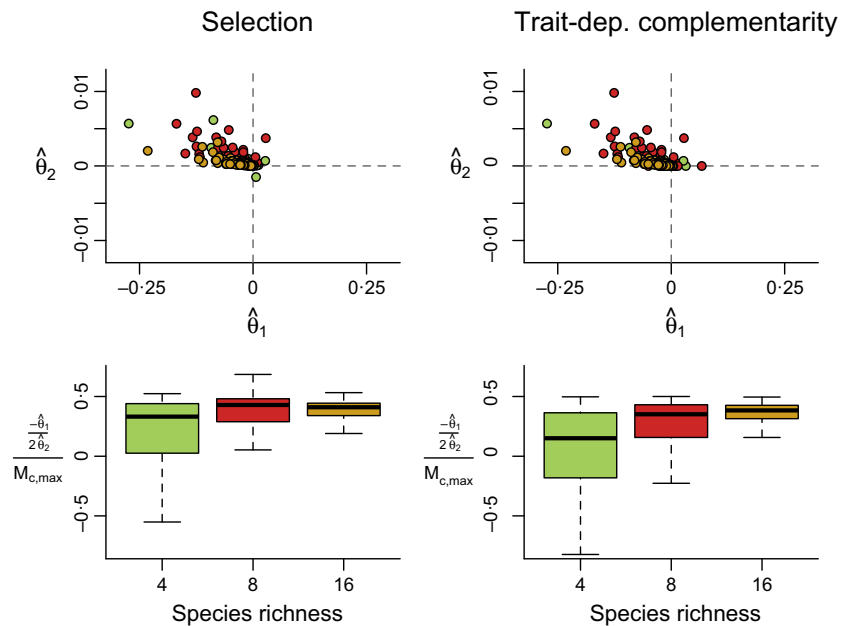


Fig. 4. Regression coefficients for second-order polynomials (upper panels) and relative position of the tip of the parabola (lower panels). Positive values in the lower panels indicate a tip of the parabola to the right of the mean monoculture yield, negative values to the left. Note that all tips are within the monoculture range, as values do not exceed 1.

monoculture functions have therefore routinely been excluded from analyses with additive partitioning, as their deviation from the null-hypothesis can easily approach infinity (e.g. Loreau & Hector 2001; Fargione *et al.* 2007). In addition, the increase in measurement error when sampling for rare species may increase the uncertainty on the deviations from the null hypothesis for species with low monoculture yields (e.g. Wisz *et al.* 2008). By splitting selection or dominance and trait-dependent complementarity effects in a linear and a quadratic term, nonlinear partitioning can mitigate these leverage problems, capturing strong deviations from the linear relationship in the quadratic term. Such strong deviations are increasingly likely to occur in systems where species strongly differ in their competitive abilities and/or when inferior competitors also have low monoculture yields and thus have very high relative yields. The problem of outliers can (partially) be circumvented using robust regression. Alternatively, functional contributions to ecosystem function can be expressed as a linear combination of multiple functional traits (Fox & Harpole 2008). The approach presented here, however, allows solving this problem, using a general function $g(\bar{M}, \Theta)$ that allows specifying an appropriate model structure. In this study, we considered the case of polynomials, but other functions could be used as well. In this study, the use of second-order polynomials sufficed to eliminate strong potential leverage problems of species that strongly deviated from the null model (Fig. 3). By splitting selection effects or dominance and trait-dependent complementarity effects in a linear and a quadratic term, nonlinear partitioning can mitigate these leverage problems, capturing strong deviations of some species in the quadratic term. Although higher order polynomials could be used, higher order terms are not only more difficult to interpret ecologically, but are also likely to over fit the data due to the low number of species generally used in biodiversity studies.

The use of null models by additive partitioning methods allows separating species-identity from biodiversity effects on function. Our results demonstrate that nonlinear deviations from these null models might be more widespread than previously considered. The nonlinear extensions of additive partitioning methods introduced here therefore increases the versatility of partitioning methods. By separating the effects of species with intermediate functional traits from species with extreme functional traits on ecosystem functioning, they allow analysing complex biodiversity effects on ecosystem functioning. In addition, they also circumvent leverage problems associated with classic partitioning methods. Nonlinear extensions can therefore be an important tool to analyse biodiversity effects on ecosystem functioning.

Authors' contributions

J.M.B. and F.D.L. conceived the idea. S.J. and M.A. derived the nonlinear extension. J.M.B. analysed the data and wrote the first draft of the manuscript. All authors contributed significantly to revisions.

Acknowledgements

J.M.B. (B1295801) and S.J. (11E2913N) are indebted to the Research Foundation Flanders (FWO) for their PhD research fellow grant. F.D.L. is indebted to the University of Namur (FSR Impulsionnel 48454E1). We thank the Cedar Creek Ecosystem Science Reserve and the University of Minnesota for providing data on the Biodiversity II experiment, which was supported by grants from the US National Science Foundation Long-Term Ecological Research Program (LTER) including DEB-0620652 and DEB-1234162. We thank Jeremy Fox for commenting on an earlier version of this manuscript.

Data accessibility

The data of the Cedar Creek biodiversity II experiment are available from the University of Minnesota Data Catalog (<http://www.cedarcreek.umn.edu/research/experiments/e120>). Analyses were performed on the plant above ground biomass data (ple120). The R code used to analyse the data is provided as online supporting information (Data S1).

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Received 24 February 2017; accepted 13 April 2017

Handling Editor: Ryan Chisholm

Supporting Information

Details of electronic Supporting Information are provided below.

Fig. S1. QQ-plots of normalized model residuals.

Fig. S2. Comparison of selection, dominance and trait-dependent selection effects between linear and nonlinear additive partitioning.

Data S1. Text file containing the annotated R script used to analyse the data.